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LATIN AMERICAN BIOGEOGRAPHY—CAUSES AND EFFECTS. INTRODUCTION[1,2,3,4]

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The 51st Annual Systematics Symposium held at the Missouri Botanical Garden, October 8–10, 2004, had as its theme *Latin American Biogeography—Causes and Effects*. The papers in this volume were either presented at the symposium or are invited papers by specialists on related topics. The fall of 2004 was an appropriate time to consider patterns of plant and animal distributions within Latin America and their affinities with other lands because it was 30 years ago, in the fall of 1974, that Raven and Axelrod published their landmark paper, "Angiosperm biogeography and past continental movements," in the *Annals of the Missouri Botanical Garden*. That paper did much to revitalize interest in biogeography and to modernize prevailing views about the physical context within which these patterns and affinities originated. It still resonates well today because it focused attention on two components essential to understanding the arrangement of organisms and communities over the landscape. One is the need for a taxonomy that reflects distributions that are biologically meaningful rather than ones that are

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[1] This and the 10 articles that follow it are the proceedings of the 51st Annual Systematics Symposium of the Missouri Botanical Garden, *Latin American Biogeography—Causes and Effects*. The symposium was held 8–10 October, 2004 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

[2] This was the 49th Missouri Botanical Garden Annual Systematics Symposium to be supported by a grant from the National Science Foundation (grant DEB-9981642). Among the many persons contributing to the planning and operation of the meeting and to the publication of the papers are Olga Martha Montiel (Center for Conservation and Sustainable Development); Mick Richardson (Research, Graduate Studies), Alina Freire-Fierro, and Sandy Lopez; Victoria Hollowell (Director, Missouri Botanical Garden Press), Carmen Ulloa Ulloa, Amy McPherson, and Beth Parada; Donna Miller and Zubin Chandran (Information Technology); William Guy (Facility Support); and Mary McNamara (registration). This symposium, together with 31 previous ones, again benefited considerably from the contributions, support, and encouragement of Peter Raven.

[3] This symposium volume is dedicated to Barbara W. Leyden, our esteemed colleague and an invited speaker to the Symposium, who died in February 2006. She established herself as an important contributor to Quaternary vegetation history and paleoecology through papers on rapid climate change and periods of aridity at glacial-interglacial boundaries in Guatemala and in the Lake Valencia Basin, Venezuela. Barbara gained further international reputation and respect for her later work on the environments of the Lowland Maya region of the Yucatán Peninsula and adjacent Central America. We join with our editor Victoria Hollowell in celebrating her critical and broad-based expertise and her vibrant contributions to the literature.

[4] The editors of the *Annals* thank Sophia Balcomb for her significant editorial contribution to these papers.

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artifacts of nomenclature. The other is the need for sound models of landscape evolution and environmental change as a context for reconstructing migrations through time.

An outgrowth of this revitalization in biogeography has been the application of new information and analysis from molecular biology (phylogeography) to augment and test long-standing knowledge derived from traditional approaches. There are now more accurate and temporally exact models of plate tectonics (Pindell, 1994; Pindell & Barrett, 1990; Mann, 1999), and there is a better appreciation of its consequences, including the direction and rates of crustal movement, the reconstruction of land bridges, the uplift of mountain systems and plateaus, and the partitioning of populations by changes in drainage systems. There is also an expanding paleontological basis for tracing the effects of these events on the distribution of lineages and communities and an increasing awareness of the impressive arsenal of techniques from independent disciplines now available for reconstructing environmental change and the biotic responses (see below).

Also important, but still in the formative stage, is development of a database of fossil plants that provides a more complete and reliable checklist of taxa and their age. Identifications of megafossils in the older literature are notoriously unreliable, as are many of the biological affinities cited in stratigraphic palynological publications for Cretaceous and Cenozoic plants. It is incomprehensible in this modern era that key information for fossil plant remains is so inaccessible. These data are badly needed for dating phylogenies, calibrating molecular clocks, and conducting studies on vicariance and dispersal. They are also valuable as historical background for formulating speciation models and in making paleoenvironmental reconstructions as analogues for the effects of current environmental trends. The online electronic framework for such databases already exists, but a coordinated effort by paleobotanists will be required to filter into the system more complete records assessed for accuracy.

The new analytical tools available, and the novel concepts being generated, are part of the reason for renewed interest in biogeography. There have been three major symposia devoted to the subject within the past three years—*Tropical Intercontinental Disjunctions*, organized by Susanne Renner and Thomas Givnish (2004); *Long-Distance Dispersal*, edited by Michael Cain, Ran Nathan, and Simon Levin (2003); and the present volume.

The goals herein are, first, to illustrate and update present and past distributions for several major groups of organisms, with particular reference to Latin America and other lands of the Southern Hemisphere. Second, to document some of the forcing mechanisms, especially plate tectonics, land bridges, and climatic change, that help explain former distributions and their residual patterns in the modern biota. Third, to show the variety of methodologies now available for documenting these forcing mechanisms and their biological consequences. The most enlightening of these methodologies often come from outside the biological sciences and include satellite imagery of atmospheric events; recent innovations in quick-time, detailed, multi-factored paleogeographic computer animations (Scotese, 2004); geochemistry; geophysics; marine sedimentology; and the myriad of factors determining weather and longer-term climate. Relationships between seemingly disparate observations are a rich source of new insights into biogeographic problems unresolved by traditional approaches. To this end, a fourth goal of the symposium was to bring together speakers not traditionally part of a single gathering to discuss results from diverse disciplines relevant to biogeography.

Consistent with these goals, the discussions begin with a summary of the biogeographic history of Gondwanan vertebrates by David Krause and others and a historical perspective of South American land mammals by Rosendo Pascual. The next papers focus on development of the land bridges that connect North and South America and the history of migrations across those bridges. Evolutionary biologist Blair Hedges summarizes current thinking about the evolution of the West Indian vertebrate fauna within that physical context, and S. David Webb reviews the Great American Biotic Interchange, bringing a lifetime of experience to interpreting the complex events that led to the formation of the Panamanian land bridge and to documenting the biological consequences of the union of South America with North America after 55 million years of separation.

More recent events and the biotic responses that modernized the landscape, environments, and communities of Latin America in the Quaternary are discussed in three papers. Sarah Metcalfe reviews information from spores, pollen, diatoms, rodent middens, dendrochronology, and deep sea cores to reconstruct fluctuations in climate for the northern deserts and the central Transvolcanic Belt of Mexico. Although the record is complex, Late Quaternary events, documented initially for the high latitudes, are shown to have affected northern and central Mexico, including a dry mid-Pleistocene, a more moist Holocene, and El Niño–Southern Oscillation (ENSO) cycles. In contrast to older views that conditions and communities became more stable and were essentially unchanged toward the tropics, a wealth of evidence now documents that the climates and biotas at the lower latitudes had a dynamic and complex Quaternary history.

Human influence becomes a factor in shaping the biotas of lowland Central America by 20,000 yr. BP, and that history is recounted by Dolores Piperno using plant microfossils, charcoal, and, innovatively, a group of plant crystals called phytoliths and starch grains of agriculturally important plants preserved on grinding tools.

One long-standing barrier to the detailed reconstruction of Quaternary vegetation history from high altitudes in the tropics has been the lack of continuous or near-continuous records. Cores from which paleobiological information on terrestrial biotas are retrieved mostly extend back only to approximately 60,000 yr. BP or less, and rarely into the previous interglacial at 100,000 yr. BP. This means that records must be spliced together from different sites and studied through a variety of techniques. The results have been less-than-consistent accounts of the climatic, biotic, and uplift history for several regions of the Neotropics (e.g., the Atacama Desert and the high elevations of Chile and Bolivia; Grosjean et al., 2003; Baker et al., 2001). This limitation was removed for one site in northern South America when cores 357 m and 586 m long, dating to 1.6 million and 3 million years, respectively, were drilled through sediments of the interandean basins around Bogotá, Colombia. These cores were obtained by a group from the University of Amsterdam and their Colombian colleagues led by Henry Hooghiemstra. The history of páramo and montane vegetation is revealed in considerable detail from Funza, and these and other studies in the northern Andes are revealing abrupt, short-term fluctuations in climate such as the Little Ice Age, Younger Dryas, Heinrich, and Dansgaard-Oeschger events long recognized in sediments from the Northern Hemisphere.

The fullest understanding of tropical ecosystems will require a seamless integration of studies on their history with those on the existing temporal versions. This synthesis has yet to be fully achieved, but there is some information on the Quaternary Atlantic Forest of Brazil (Ledru et al., 2005). This will complement nicely the studies of Rodolphe Spichiger and others (e.g., Perret et al., this volume) on the biogeographic history of the Gesneriaceae in the Atlantic Forest via dispersal-vicariance analysis.

My own contributions on the geologic record of the Rhizophoraceae and on the origin of African–South American biotic affinities make two points not widely emphasized in the current biogeographic literature. With reference to the history of *Rhizophora* in the Caribbean region, it is clear from the extensive fossil pollen record that the genus first appears at the middle to late Eocene transition (ca. 45 million years ago) and has been more or less continually present ever since. One interpretation of the emerging molecular evidence is that, rather than distributional and taxonomic stasis, the genus disappeared for an estimated 3 million years between ca. 14 and 11 million years ago, and that the modern black mangroves are derived from progenitors that arrived ca. 11 million years ago. It is possible that both results are valid because the stenopalynous pollen establishes the presence of *Rhizophora*, as a genus, continuously in the region for 45 million years, but does not preclude the extinction and re-introduction of the molecular-defined extant lineages throughout this interval. A duality of stasis versus more dynamic change will likely become commonplace as paleobiogeographic patterns and evolutionary histories from the fossil record and from molecular data are compared.

My other contribution involves a synthesis of observations from different disciplines regarding the increasing number of elements that are recognized as having migrated between Africa and the Caribbean/South American region. This interchange has been accomplished in a variety of ways, including vicariance in Cretaceous and Paleocene times, expressed primarily at the higher taxonomic categories; direct overland migration across the North Atlantic land bridge until about the middle Eocene; and long-distance dispersal occurring throughout this time but becoming essential after about the middle Eocene. The relative importance of these overlapping modes depends on the dispersal potential of the propagules, the ecological requirements of the migrants, the time during which the lineage under consideration has been in existence, and the physiographic and climatic conditions prevailing in the region being transversed at the time the migrations occurred. Observations relevant to long-distance dispersal between Africa and South America are: (1) the enormous quantities of dust and organic debris being blown from the Sahara and Sahel into the Caribbean region, especially during periods of major hurricanes; (2) the increase in hurricane intensity, and possibly hurricane frequency, with global warming; and (3) the existence in the geologic past of intervals when global temperatures were considerably warmer than at present (e.g., during the early Eocene climatic optimum and in the middle Pliocene: Schmitz et al., 2000; Cronin & Dowsett, 1991). Furthermore, the Eocene was the time of emergence of the Greater Antilles, and the distance between Africa and South America was about one-half to one-third less than at present. Thus, the opportunity for wind transport for some organisms and/or their propagules may have been greater during these peaks of warmth than would seem plausible under modern conditions. There are extant plant genera in which molecular evidence suggests disjunctions between Old World and New World taxa originated ca. 3–4 million years ago (viz., in the middle Pliocene; Graham, this volume).

Collectively, the papers of the symposium illustrate some of the past and present characteristics and affinities of the Latin American biota and the causes leading to its modernization. Interwoven throughout are examples of the various techniques being utilized to reveal their history. This record is becoming increasingly recognized as important to understanding the origin, development, and functioning of the present faunal and floristic communities and in anticipating future environmental and biotic change. To emphasize the considerable array of techniques available for investigating the historical aspects of ecosystems, the following list augments the approaches noted in the papers of this volume (see also Graham, 1999: chapter 4—Methods, Principles, Strengths, and Limitations):

(1) It is now possible to determine the concentration of CO_2 and other greenhouse gasses in the Earth's atmosphere over the past 100 million years, correlate the fluctuations with temperature trends based on oxygen isotope ratios, date the events through paleomagnetic and biostratigraphic studies, and relate the reconstructed climate to the history of lineages and communities. This is accomplished by such diverse techniques as analyzing gas in air bubbles trapped in ice and by calculating the changing mass of the Earth's carbonate sediments through time. It is also possible to calibrate the stomatal index of leaves from extant plants growing in environments of known CO_2 concentration, as well as from herbarium sheets, and to apply the indices to fossil cuticles of different ages. In this way, past concentrations can be estimated, and the fluctuations can be compared with temperature trends from oxygen isotope studies in the marine realm and with vegetational histories from the terrestrial environment.

(2) Changes in albedo (reflectivity), precipitation, carbon storage (sinks), and carbon release (pumps) can be estimated for various vegetation types (e.g., tundra, boreal forest, tropical rain forest, tropical savannas) and the climatic implication assessed as vegetation is cleared or as one vegetation type (e.g., lowland rain forest) is replaced by another (e.g., caatingas/cerrado) over geologic time. Alterations in plant cover are an important feedback to climate because, for example, half of the precipitation over the rain forest is generated by the forest itself (Clapperton, 1993).

(3) The amounts of insolation can be calculated for specific places and times as the Earth changes position relative to the sun (the Milankovitch cycles). It is also known that the solar constant (2 cal/cm^2/min) has varied over time, and although these fluctuations cannot be precisely quantified and do not seem to vary in concert with extinctions, evolutionary peaks, or migrational histories, they constitute a dampening or amplifying overlay to the Milankovitch variations and other climate-forcing mechanisms.

(4) The height of mountains at various points in time can be estimated by calculating the mean annual temperature of time-equivalent fossil floras from sea level and from high elevations using the modern analogue method and/or leaf margin analysis (Gregory-Wodzicki, 2000; Graham et al., 2001). By applying the average global lapse rate of 6 C/km, an approximation of the altitude of the highland flora can be made. These estimates, together with other geologic information, have revealed that about half the elevation of the Central Andes has been attained in relatively recent times (viz., since the late Miocene). That has implications for such topics as the time of origin of páramo environments and vegetation, speciation by vicariance in the region, and the migration of temperate and high-altitude organisms along the axis of the high Andes.

(5) The growth of stalagtites, and the midges and mites they often contain, is being used to estimate precipitation history in the deserts of the southeastern United States, in adjacent northern Mexico, and in Brazil (e.g., Polyak et al., 2001).

(6) Amino acid racemization in radiocarbon-dated emu eggshell fragments is a function of temperature, and it is being used to reconstruct climates in parts of the Southern Hemisphere (Johnson et al., 1999).

(7) Alkenones are long-chained organic molecules from algae that preserve in ocean sediments as biochemical fossils. The degree of unsaturation is temperature sensitive (increasing unsaturation indicates cooling water), and this affords a method of detecting El Niños during times beyond historical records. The modern cycle of El Niños along the Peruvian coast appears to have begun ca. 5800 yr. BP, and it corresponds to a time of intense monument building, while the onset of even stronger events corresponds to their abandonment.

(8) The solubility of noble gases is dependent on the temperature of the water, and ^{14}C-dated samples from groundwater in Brazil indicate a cooling of 5 C at the Last Glacial Maximum ca. 18,000 yr. BP. This is one example from a wealth of new information that indicates lowland Amazonia experienced significant cooling during the Quaternary. Whether it also experienced drying and, if so, when, where, and to what extent, is still unknown despite proclamations to the contrary in the much-debated issue of refugia.

(9) Titanium is a terrestrial mineral that is found in offshore basins of Venezuela. Decreases in the amounts along sections of marine cores reflect periods of reduced runoff and river flow, and it is one indication of aridity associated with cooling in Amazonia during intervals of the Quaternary.

(10) Geographical information systems (GIS) tools, remotely sensed data, and niche modeling techniques are being integrated with botanical data to study the ecology and evolution of plant geographic ranges and spatial patterns of diversity (Trisha Consiglio, Analysis Unit, Center for Conservation and Sustainable Development, Missouri Botanical Garden; pers. comm., 2006).

These and other techniques demonstrate how far we have come since the early great synthetic minds of biology laid the foundations of biogeography. Linnaeus, through the 186 dissertations of the *Amoenitates Academicae*, noted that the vegetation of distant regions showed floristic similarities (e.g., Kamchatka and eastern North America in the 1750 dissertation of Jonas P. Halenius); that is, there were patterns in the arrangement of organisms over the landscape. Von Humboldt established in 1807, from his observations in the Ecuadorian Andes, that vertical changes in communities along mountain slopes were comparable to horizontal changes with latitude. He concluded that climate is an important factor in determining these patterns, and that did much to place the study of biogeography on a scientific basis. More recently, the consideration of time and the occurrence of past events has become increasingly recognized as an essential component of biogeography, as it was when geologist Lyell implanted the concept that lineages and communities extend back through time in the thinking of Darwin and Wallace on evolution. The papers presented here, and in other recent symposia, are a statement of the progress being made in understanding the causes and the implications of plant and animal distributions. The likes of Linnaeus, Von Humboldt, Darwin, and Lyell would undoubtedly be amazed and immensely pleased.

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